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Cover photography: Whooper Swans *Cygnus cygnus* arriving at Martin Mere, England. Photo: Paul Marshall. (www.paulmarshallphotography.com)

Crossing the ultimate ecological barrier: evidence for an 11 000 km long non-stop flight from Alaska to New Zealand and eastern Australia by Bar-tailed Godwits *Limosa lapponica*

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ABSTRACT

Populations of the Bar-tailed Godwit *Limosa lapponica* embark on some of the longest migrations known among birds. The *baueri* race breeds in western Alaska and spends the non-breeding season a hemisphere away in New Zealand and eastern Australia; the *menzbieri* race breeds in Siberia and migrates to western and northern Australia. Although the Siberian birds are known to follow the coast of Asia during both migrations, the southern pathway followed by the Alaska breeders has remained unknown. Two questions have particular ecological importance: (1) do Alaska godwits migrate directly across the Pacific, a distance of 11 000 km; and (2) are they capable of doing this in a single flight without stopping to rest or refuel? We explored six lines of evidence to answer these questions. The distribution of resightings of marked birds of the *baueri* and *menzbieri* races was significantly different between northward and southward flights, with virtually no marked *baueri* resighted along the Asian mainland during southward migration. The timing of southward migration of the two races further indicates the absence of a coastal Asia route by *baueri*, with peak passage of godwits in general occurring there a month prior to the departure of most birds from Alaska. The use of a direct route across the Pacific is also supported by significantly more records of godwits reported from within a direct migration corridor than elsewhere in Oceania, and during the September to November period than at other times of the year. The annual but rare occurrence of Hudsonian Godwits *Limosa haemastica* in New Zealand and the absence of records of this species along the Asian mainland also support a direct flight, and are best explained by Hudsonian Godwits accompanying Bar-tailed Godwits from known communal staging areas in Alaska. Flight simulation models, extreme fat loads, and the apparent evolution of a wind-selected migration from Alaska further support a direct, non-stop flight.

Note: This paper is an abbreviated version of the original that appeared in the February 2005 issue of The Condor.

INTRODUCTION

The timing of human settlement of the Earth's biomes appears to be related not only to the physical extent of ecological barriers encountered but also to their inhospitable nature. In this sense, the Pacific Ocean arguably represents the most formidable ecological barrier, with human expansion into the far reaches of Oceania occurring only within the past 3 000-4 000 years (Hurles *et al.* 2003). But does the Pacific Ocean present a similar ecological barrier to birds? Obviously not to those forms adapted for existence on and from the sea. And surprisingly it appears not to for many land-birds, as more of these species have migrations crossing portions of the Pacific than across any other ocean (Williams & Williams 1999). For example, several species of shorebirds migrating from Alaska must cross a minimum of 3 500 km of open ocean before reaching Hawaii, and even large portions of these populations overfly the Hawaiian Archipelago en route to the next available land 3 000 km farther south (Thompson 1973, Williams & Williams 1988, 1990, 1999, Marks & Redmond 1994, Johnson 2003). The limits of such non-stop flights are pushed even further by Red Knots *Calidris canutus* and Bar-tailed Godwits *Limosa lapponica* that migrate northward from south-eastern Australia and New Zealand to staging sites along the coast of the Yellow Sea, a distance of over 8 000 km (Battley 1997, Battley & Piersma 2005, J. Wilson and C. Minton unpubl. data).

Two subspecies of the Bar-tailed Godwit occur in the central Pacific basin (Higgins & Davies 1996, Engelmoer & Roselaar 1998, McCaffery & Gill 2001). The *L. l. menzbieri* population breeds in central northern Siberia and spends the non-breeding season in western and northern Australia. Members of the *L. l. baueri* population nest in Alaska and spend the non-breeding season in New Zealand and eastern Australia. In the Anadyr Basin area of Chukotka, there is a third, much smaller breeding population of unresolved taxonomic affinity (Engelmoer & Roselaar 1998, see Discussion). The *menzbieri* population, numbering about 170 000 birds, appears to migrate both north and south in a two-stage flight with the leg from western Australia to the Yellow Sea and Korean Peninsula entailing a 6 000 km-long non-stop effort (Barter & Wang 1990, Wilson & Barter 1998, J. Wilson and C. Minton unpubl. data), and the southward leg an 8 000 km-long flight from the Sea of Okhotsk (M. Barter pers. comm.). The *baueri* population is slightly smaller (Gill & McCaffery 1999, McCaffery & Gill 2001, Minton in press), and during northward migration birds are thought to undertake a single flight of between 5 000 and 8 000 km (Riegen 1999, J. Wilson and C. Minton unpubl. data). The advent of intensive marking programs initiated

in New Zealand and Australia in the late 1970s (Riegen 1999, J. Wilson and C. Minton unpubl. data) has shown that birds marked within the non-breeding range of *baueri* do not occur along the Asian coast during southward migration. This led Barter (1989) and others (Barter & Wang 1990, Riegen 1999, J. Wilson and C. Minton unpubl. data) to speculate that the southward flight is instead direct across the Pacific, a minimum distance of about 9 700 km to north-eastern Australia and 10 800 km to New Zealand.

Mäori folklore lends support to godwits crossing this large ecological barrier. When living on a small Pacific island north of New Zealand, they noticed that the küaka (Bar-tailed Godwit) migrated every year in a southerly direction. From this evidence, they deduced that land was to be found to the south, and canoes were outfitted for a voyage that eventually led to the discovery of Aotearoa (New Zealand), their new home (Gudgeon 1903, Te Paa 1912, Phillipps 1966, Riley 2001).

Building upon these millennia-old observations, our objective here is to answer two fundamental and oft-pondered questions concerning the southward migration of the *baueri* race of the Bar-tailed Godwit: (1) do birds migrate across the Pacific Ocean between Alaska and New Zealand, a distance of 11 000 km, and (2) are they capable of doing this in a single flight without stopping to rest or refuel? We address these questions by exploring six lines of evidence: (1) distributional records and chronology of occurrence of godwits during migration periods; (2) differential resighting rates of leg-flagged birds seen during northward and southward migrations; (3) comparisons between departure and arrival events recorded at migration termini; (4) annual occurrence of a congener, the Hudsonian Godwit *L. haemastica*, in Oceania; (5) analyses of maximum flight ranges; and (6) synoptic weather and wind-field analyses across the Pacific and atmospheric trajectory models at the time of known departures from Alaska.

METHODS

Distributional records and chronology throughout Oceania

If godwits undertake a direct trans-Pacific flight from Alaska to New Zealand and eastern Australia, they would be expected to occur in central Oceania either as occasional fall-outs from migrating flocks or at regularly used stopover sites. To assess this, we turned to three principal sources (see Gill *et al*. 2005 for details). Combined, they represent over 300 field assessments (with 568 monthly records) collected since the early 1920s (see Gill *et al*. 2005 for assumptions).

We also assessed seasonal occurrence from census data obtained at sites where counts have been conducted throughout the annual cycle (Gill *et al*. 2005).

Band recoveries and sightings of leg-flagged birds

We used band recovery and resighting data to assess seasonal migration routes of godwits. The banding databases for godwits contain a combined total of about 14 000 records, including about 10 000 since the early 1980s representing birds on which various colors of leg flags, specific to individual countries or regions, were applied. Much of the information for godwits has previously been summarized by Riegen (1999), Minton *et al*. (2002), and J. Wilson and C. Minton (unpubl. data). Almost annually since the mid-1990s, there have been efforts dedicated to observing marked godwits, both on the migration staging grounds in Alaska (Gill & McCaffery 1999) and at migration stopover sites in Japan, Korea, and China (J. Wilson and C. Minton unpubl. data).

Timing of arrival and departure

To assess levels of concordance between periods of departure and arrival, we relied on available seasonal census data from breeding, non-breeding, and migratory stopover sites of both the *baueri* and *menzbieri* subspecies. Most of these studies were conducted independently of each other and focused on site-specific issues and not broad geographic regions or range-wide assessments. Nevertheless, they are of sufficient number and scope that comparisons can be made, especially within the past decade, when we made concerted efforts to document departures from Alaska and arrivals in New Zealand.

Maximum flight range predictions

For an energy-based evaluation of the proposed 11 000 km-long trans-Pacific flight by godwits, we computed maximum flight ranges (i.e. the distance flown in still-air conditions until the fuel store is depleted) and changes in other variables using an advanced program that encompasses the family of flight-mechanic models presented in Pennycuick (1989). These were later modified to account for use of protein stores during long-distance flights (Pennycuick 1998). The variables used in program FLIGHT and assumptions we make for several of these variables are presented in Table 1 of Gill *et al*. (2005).

Environmental data

In the previous predictions, we assumed that flight speed was unaffected by winds, but a number of waterbird species staging in south-western Alaska have been shown to have wind-aided southward migrations (see Discussion). To learn if departures of godwits from Alaska were correlated with weather, we looked at synoptic weather and wind-field data from the September-November migration period. From this, we wanted to learn not only what weather characteristics were associated with known departure events, but also the frequency, intensity, and track of storms that occurred throughout the North Pacific during the staging period. This investigation also lead us to look at en route winds, both those associated with departures and those across the central and southern Pacific Ocean. To learn the extent of favorable winds provided by storms during departure, we used a Lagrangian atmospheric trajectory model (CMC 2001).

To assess winds over the Pacific Ocean once birds had departed on migration, we used two sources. For the observed departure in 1987, we obtained data (2.5° latitude x 2.5° longitude grid) from the NOAA-CRIES Climate Diagnostic Center (CDC 2004); for all other departures, we used data (presented by 0.9° x 0.9° grid) from the CMC Global Data Assimilation and Forecast System (CMC 2004). (For this effort, both have been converted to a 10° x 10° grid). Even though it is unlikely that birds migrate at a constant altitude, we simplified our analysis by selecting winds at the 850 mb (c. 1 500 m) level, a general height at which shorebirds in other studies have been shown to migrate (citations in Green 2003). See Gill *et al*. (2005) for additional details.

Statistical analyses

Reported values are means ± SD. For assumptions associated with various statistical tests, see Gill *et al*. (2005).

Table 1. **Variables used in the simulation of flight ranges (distance to depletion of fuel store) for male Bar-tailed Godwits *Limosa lapponica* departing Alaska on an 11 000 km-long flight[a] to New Zealand and eastern Australia (Program Flight, version 1.15).**

Variables (SI-units)	Values
General assumptions[b]	
Basal metabolic rate equation[c]	for non-passerines
Induced power factor	1.2
Profile power ratio	0.903
Acceleration due to gravity (m sec^{-1})	9.81
Fat energy density (J kg^{-1})	$3.90 * 10^7$
Dry protein density (J kg^{-1})	$1.83 * 10^7$
Protein hydration ratio[d]	2.2
Conservation efficiency	0.23
Circulation and respiration factor	1.1
Density of muscle (kg m^{-3})	1 060
Mitochondria inverse power density (m^3 W^{-1})	$1.2 * 10^{-6}$
Power density of mitochondria	constant
Specific assumptions[e]	
Altitude of flight (m)	0 or 1 500
Air density (kg m^{-3})	1.23
Starting ratio $V:V_{mp}$	1.2
Flight speed during trip[f]	constant
Specific work	constant
Minimum energy from protein (%)	5
Body drag coefficient	0.1 or 0.05
Bird-related measurements	
Wing span (m)[g]	0.73
Aspect ratio[h]	9.3
Wing area (m2)[i]	0.0573
Body mass at start (g)[j]	455, 485, or 515
Fresh mass of pectoral muscle at start (g)[j]	67, 72, or 76
Fat mass at start (g)[j]	always 200
Airframe mass at start (g)[j]	188, 213, 239

[a] The great circle distance between the most northerly Alaska staging site (Yukon Delta) and the northern tip of New Zealand is 10 700 km; that between the most southerly staging site (Nelson Lagoon) and northern Queensland, Australia, is 9 700 km. We assume godwits follow a great circle route (orthodrome), although a constant compass course (loxodrome route) would likely add little additional distance since the departure and arrival sites occur along a north-south axis.

[b] Based on standard settings in the program Flight and as verified by Pennycuick & Battley (2003).

[c] Changing it to the passerine equation in view of high BMR in many shorebirds (Kersten & Piersma 1987) has remarkably little effect on the model outcomes (see program FLIGHT).

[d] This is the ratio of water released and lost through respiration as dry protein is combusted, assuming that water makes up 69% of wet protein.

[e] Specific to southward migrating *baueri* godwits, with the body drag coefficient and altitude being varied.

[f] Flight speed (i.e. true air speed; see program FLIGHT) is a function of the starting body mass.

[g] Based on a sample of 26 male *baueri* godwits from non-breeding grounds in New Zealand (Battley & Piersma 2005).

[h] Based on a sample of wing tracings of three *baueri* godwits from Alaska (C. J. Pennycuick pers. comm.).

[i] Computed from wing span and aspect ratio.

[j] Based on a variety of body mass and body composition values.

RESULTS

Seasonal occurrence, distribution, and numbers of birds in Oceania

We found records of godwits in Oceania during every month of the year (Fig. 1A), but most frequently during the southward migration period (September-November) when 49% of all monthly records ($n = 254$) are attributed. No other month accounted for more than 8% of the total. We found a similar temporal pattern at Suva Point, Fiji, the only site in Oceania at which systematic counts of godwits have been conducted for extended periods (Fig. 1B).

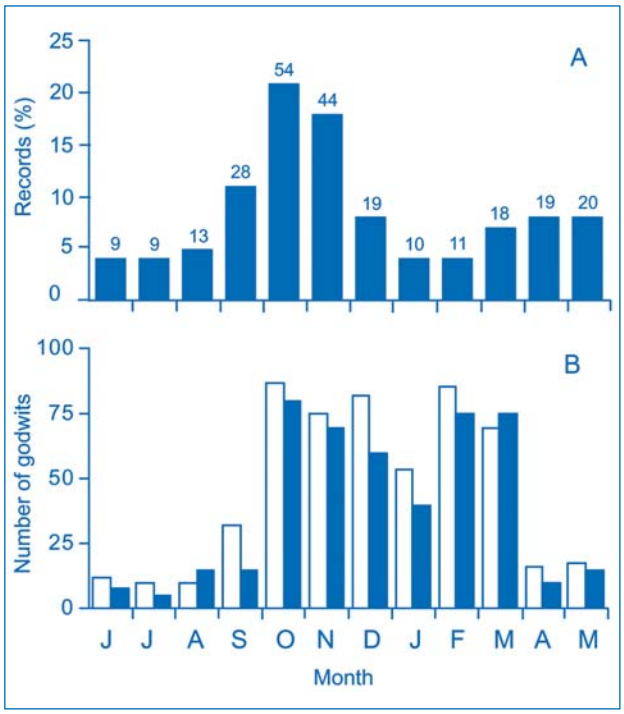

Fig. 1. (A) Percentage of total records of occurrence ($n = 254$) of Bar-tailed Godwits *Limosa lapponica* throughout Oceania each month. Numbers above bars show number of records. (B) Number of godwit records during monthly censuses at Suva Point, Fiji; solid bars from Skinner (1983) and open bars from D. Watling (unpubl. data).

The geographic occurrence of godwits in Oceania was widespread, with birds noted from most (77%) of the 30 major archipelagoes and from over 350 different atolls and islands within. Only from central and eastern Polynesia (e.g. Southern Cook, Marquises, Austral, Gambier, Line, most of the Tuamotu, and Pitcairn islands) have birds not been recorded.

We also found a significant difference between the southward migration period and the rest of the year ($21 = 32.4$, $P < 0.001$) when we looked at geographic distribution of records in Oceania by season. Most sites where godwits were recorded during the September-November period occurred throughout a corridor linking Alaska and the non-breeding grounds in eastern Australia and New Zealand (Fig. 2). The same pattern was found when total maximum counts per site were compared inside and outside the migration corridor. When adjusted for sites with multi-year records, 93% ($n = 868$) of all godwits noted during the southward migration period came from sites within the likely migration corridor. The proportion increased to 97% when records just outside but east of the corridor (Hawaiian and Cook

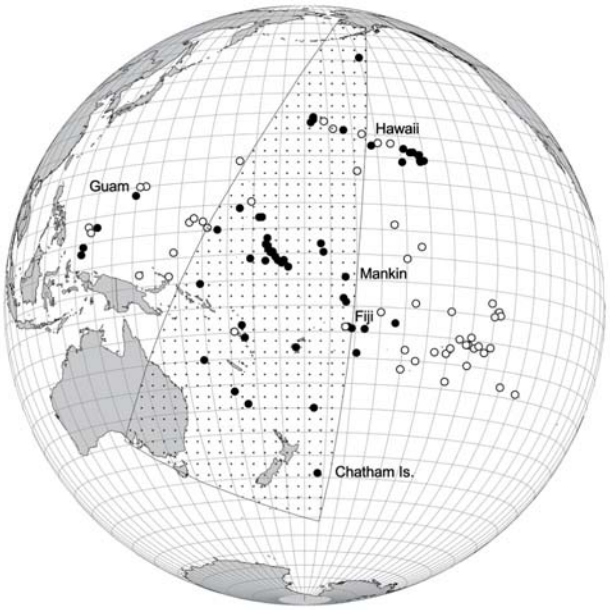

Fig. 2. Distribution of records of Bar-tailed Godwits *Limosa lapponica* throughout Oceania during the southward migration period (September-November). Filled circles = sites reporting godwits; unfilled circles = sites at which no godwits were noted during the period. Map projection = Orthographic (central meridian = 180; reference latitude = –10). Lateral bounds of stippled region = plotted great circle routes.

islands) were also considered (Fig. 2). Most (87%) of the 868 birds were recorded from four sites in the southern half of the migration corridor: Mankin Atoll (120 birds) in the Tungaru Islands, Rewa River (200 birds) and Suva Point (121 birds) in Fiji, and Chatham Island (314 birds) east of New Zealand (Fig. 2). When these four sites are not considered, the average maximum number of godwits recorded at sites elsewhere in Oceania during southward migration was similar both outside (4.6 ± 7.1, range 1–21) and inside (2.8 ± 3.9, range 1–20) the corridor (Mann-Whitney *U*-test: z = 0.9, n = 13, 37, P = 0.19).

Resightings of marked birds

The proportions of color-flagged godwits of the two subspecies that were resighted along the coast of Asia during northward and southward migrations differed markedly (Table 2; χ^2_1 = 36.8, $P < 0.001$). On northward migration, both *baueri* and *menzbieri* regularly used intermediate stopover sites; during southward migration, however, *menzbieri* were still commonly sighted along the coast of Asia whereas *baueri*, with but three exceptions, have gone unreported. Sightings of marked *baueri* (n = 136; R. Gill and B. McCaffery unpubl. data), but not of marked *menzbieri*, on the Alaska staging grounds from late August through September (1999-2004) further indicate the extent of separation of the two subspecies during southward migration.

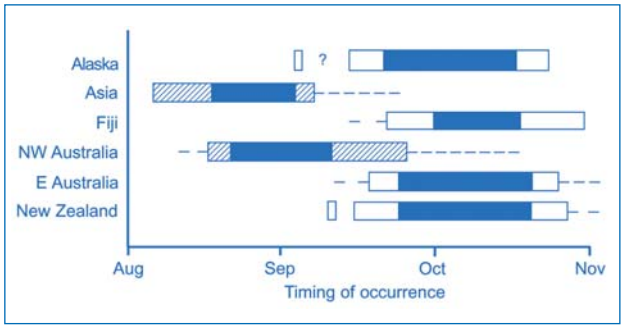

Fig. 3. Timing of southern passage of Bar-tailed Godwit *Limosa lapponica* races *baueri* (unfilled bars) and *menzbieri* (cross-hatched bars) at different locations along their migration route. Filled portions of bars indicate periods of peak passage; dashed lines indicate periods of movement. See Gill *et al.* (2005) for sources.

Timing of departure and arrival

The average peak departure of godwits from Alaska and peak arrival in Fiji, New Zealand, and south-eastern Australia occur within a two- to three-week period from late September to mid-October (Fig. 3). Both departure from Alaska and arrival in New Zealand can be earlier, however, as recorded in 2003, when birds were seen leaving during the first week of September (Table 3) and the first arrivals were noted in New Zealand 6-10 days later (A. Riegen and P. Battley unpubl. data). In contrast, the southward passage of *menzbieri* godwits along the coast of Asia and arrival in Western Australia is a month earlier and essentially over before *baueri* godwits depart Alaska (Fig. 3).

Table 2. Seasonal distribution of resightings and recoveries of the *baueri* and *menzbieri* subspecies of the Bar-tailed Godwit *Limosa lapponica* along the coast of East Asia during the northward and southward migration. All putative *baueri* were marked on the non-breeding grounds in New Zealand and eastern Australia; *menzbieri* were marked in western Australia (but see footnotes for the few exceptions). See Gill *et al.* (2005) for sources of data.

	Northward		Southward	
Sighted in	***baueri***	***menzbieri***	***baueri***	***menzbieri***
Russia	2	3	2	5
Japan	84[a]	1		2
North Yellow Sea	18	38	1	2
Republic of Korea	62	54		35
Hong Kong, Taiwan, SE China[b]	2	52		1
Total	**168**	**148**	**3**	**45**

[a] Includes one bird flagged in Japan in August and seen in New South Wales, Australia, in the subsequent February.

[b] Includes 40 birds (one *baueri* and 39 *menzbieri*) shot by hunters; the remainder are resightings of flagged birds including one juvenile flagged in Hong Kong and recovered in north-western Australia.

Table 3. Conditions during departures of Bar-tailed Godwits *Limosa lapponica* on southward migration from sites on the Alaska Peninsula.

		Storm characteristics			Departure site winds		Tail-wind component[d]		
Departure period[a]	No. birds (no. flocks)[b]	Low center position	Pressure (mb)	Distance & direction[c] from departure point	Speed (m sec^{-1})	Direction	Speed (m sec^{-1})	Direction	Fetch (km)[e]
20 Oct 1987 (09:30)	>9 (?)	47°N, 174°W	976	1 100 km; 225°	10	N	10–21	NNW-NW	1 200
24 Sep 1996 (03:00–07:00)	492 (1)	43°N, 175°W	974	1 650 km; 237°	4–8	NNE	8–23	N-NW	1 300
10–11 Oct 2000 (04:00–20:00)	>4 000 (?)	55°N, 160°W	986	650 km; 184°	5–10	NNE	13–23	N-NW	900
3–5 Sep 2003 (09:00–10:00)	5 090 (15)	47°N, 162°W	998	900 km; 183°	0–5	N	8–15	N-NNW	1 100

[a] 1987 departure point: Cold Bay (55°20'N, 162°50'W); 1996 and 2000: Nelson Lagoon (56°00'N, 161°00'W); 2003: Egegik Bay (58°10'N, 157°30'W). All times Coordinated Universal Time (add 10 hr for local, Alaska Daylight Time).

[b] For details of 1987 departure see Piersma & Gill (1998); 1996 observation by R. Gill and M. Owens; 2000 observation by R. Gill; 2003 observation by R. Gill and D. Ruthrauff.

[c] Direction relative to true north from departure site.

[d] Winds along likely initial migration route from departure site.

[e] Fetch = longest distance with sustained winds from tail or quartering tail direction.

Table 4. Predicted performance (according to program Flight) of male Bar-tailed Godwits *Limosa lapponica* initiating flight with given fuel stores and flight parameters (see Table 1) and flying until fat stores are depleted. Program FLIGHT assumes that a small part of the energy used comes from burning protein, primarily from pectoral muscle but also from other components of lean mass as well (see Methods for specifics).

	At start of flight				At fat depletion				
Body drag coefficient	Body mass (g)	Lean mass (g)	Fat mass (g)	Pectoral muscle mass(g)	Body mass (g)	Pectoral muscle mass (g)	Distance covered (km)[a]	Days in the air	Air speed (m sec^{-1})
0.10	455	255	200	67	183	28	9 303	7.0	15.3
0.10	485	285	200	72	213	32	8 154	6.0	15.6
0.10	515	315	200	76	243	36	7 240	5.3	15.9
0.05	455	255	200	67	188	30	12 883	8.2	18.2
0.05	485	285	200	72	214	33	11 308	7.0	18.6
0.05	515	315	200	76	244	37	10 049	6.1	19.0
0.05	485	285	200	54	213	24	11 308	7.0	18.6
0.05	515	285	230	76	202	29	12 928	7.9	19.0

[a] Distances covered based on flight at sea level.

Maximum flight range predictions

With a starting body mass of 485 g, a fat mass of 200 g (= 41% body fat), and pectoral muscles adjusted to body mass, male Bar-tailed Godwits would be able to cover 11 000 km under still air conditions only if their body drag coefficient would be as low as 0.05 (Table 4, Fig. 4). Under either assumption for body drag, arrival body mass (213–214 g, or 75% of the lean mass at start) would be reasonable. (Note that Battley *et al*. 2000 found lean mass of Great Knots *Calidris tenuirostris* that arrived after a 5 400 km long flight to be c. 80% of lean mass at departure). Pectoral muscle masses of godwits at arrival (21-33 g) were small, but not unrealistically so (Landys-Ciannelli *et al*. 2003). A body drag coefficient of 0.05 appears to be realistic for godwits, since it produces a more consistent prediction of air speed (18.6 m sec^{-1}, or 67 km hr^{-1}), i.e. a value that is much closer to empirical values obtained by radar for godwits of the *L. l. taymyrensis* subspecies during northward migration (18.4 m sec^{-1}; M. Green and T. Piersma unpubl. data), than for air speeds (15.6 m sec^{-1}) obtained with a body drag coefficient of 0.1 (Table 1).

Reducing body mass by 30 g and leaving fat mass at 200 g (44% fat) enhanced the predicted maximum flight range (Fig. 4), but led to inappropriately low arrival masses and very small pectoral muscle masses (Table 4). Increasing body mass by 30 g lean tissue (39% fat) led to lower maximum flight ranges but also to reasonable values for remaining body and pectoral muscle masses at the point of fat depletion (Table 4). When we decreased pectoral muscle mass at departure to 54 g based on the fraction of body mass measured in the sample of *baueri* from New Zealand (0.111; Battley & Piersma 2005), final body mass was of the right order but pectoral muscle mass (24 g) remaining after the flight was certainly too low (Table 4). When we gave birds with a lean mass of 285 g an extra 30 g of fat (thus

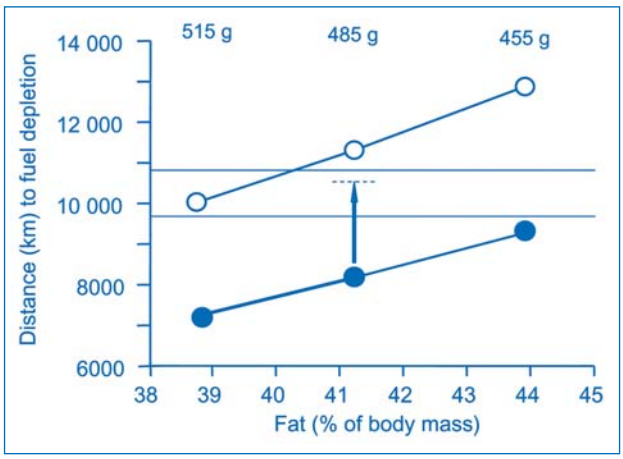

Fig. 4. Predicted maximum flight range (the distance to fuel depletion) in male Bar-tailed Godwits *Limosa lapponica*. Plot is a function of body mass (515, 485, or 455 g), variation in the percent fat of body mass at the start of the flight from Alaska (39-44%; with correlated variation in body mass, fat-free mass, and pectoral muscle mass, but with a constant fat load of 200 g), and two values for body drag coefficient (BDC). Solid circles indicate simulations using a BDC value of 0.1; unfilled circles indicate simulations using a value of 0.05. The solid horizontal lines represent great circle distances transited by godwits: the upper line at 10 800 km is the distance between the northernmost staging site in Alaska (Yukon Delta) and the northern tip of North Island, New Zealand; the lower line at 9 700 km is the distance between the southernmost staging site in Alaska (Nelson Lagoon) and Townsville, Queensland, Australia, the suspected northern portion of the non-breeding range of *baueri* in Australia. For a bird with a starting body mass of 485 g, a BDC of 0.1, an average constant flight speed of 15.4 m sec^{-1}, but with an average tail wind of 4.5 m sec^{-1} for the entire distance, the flight range would be increased by 2 000 km, as indicated by the arrow and broken horizontal line. A similar proportional increase in flight range would occur in birds having a BDC of 0.05 (unfilled circles).

increasing pectoral muscle mass from 72 g to 76 g), they increased their maximum flight range, but reduced final body mass and pectoral muscle mass to quite low values.

Departures in relation to weather

Actual departures of birds on southward migration from Alaska were observed on four occasions between 1987 and 2003 (Table 3; Gill *et al*. 2005). Observed departures spanned almost a seven-week period between early September and mid-October (Table 3). All four events occurred in association with moderate troughs with imbedded storms having central pressures between 976 and 998 mb (average 984 mb) and centered between 650 and 1 400 km south of the departure sites (Table 3, Fig. 5). Such storms are propagated in the Aleutian low pressure system along a track that, beginning in September, passes south along the Aleutian Islands and then northward into the Gulf of Alaska. During the period 1976-2000, storms with central pressure of between 975 and 1 000 mb occurred annually along this track on average twice in September, between two and three times in October, and just over three times in November. Local winds during the departure events varied in both direction and intensity, ranging between 0 and 10 m sec^{-1} from north to north-east. The positions of the storm centers at the time of departure (Fig. 5) suggest that birds would have to have flown on a slight west-south-west heading (200-240°) before obtaining maximum benefit from tail winds, but once positioned within the "upstream" side of the systems, birds flying in a southerly direction would have encountered strong direct to quartering tail winds averaging 15 m sec^{-1} (mid-point of ranges, Table 3). Winds of this approximate speed and direction would have been maintained on average over a distance of about 1 000 km, with conditions associated with the 1996 departure, for example, extending almost 1 500 km south (Table 3, Fig. 6).

Winds during the mid-portion (latitudes 20° N to 20° S) of each of the four suspected flights (Fig. 5) were very similar and characterized by light (2-8 m sec^{-1}) crosswinds or quartering tail to head winds. Once into the southern realm of the south-east trades and austral westerlies at about days five and six of the flight, godwits again experienced strong direct tail or quartering tail winds over the last 1 000 km of the flight, especially if New Zealand was the destination. Any birds attempting to go to eastern Australia during the 2003 event would have experienced moderate to strong head winds from central Queensland south to Victoria, but mostly calm winds if landfall were in northern Queensland (Fig. 5).

DISCUSSION

The evidence we present supporting a direct non-stop flight by *baueri* godwits between Alaska and New Zealand is straightforward and compelling: (1) *baueri* godwits are extremely rare along the central East Asian mainland on southward migration; (2) peak southward departure from Alaska and peak arrival in New Zealand occur within the same relatively short period, and both are a month later than for godwits (*L. l. menzbieri*) that do follow a continental Asia route; (3) too few godwits have been noted in Oceania to suggest any regularly used intermediate stopover site(s), but the birds that are recorded there peak in occurrence and number in October and within a direct corridor linking Alaska and New Zealand/eastern Australia when fallout of transients would be expected; (4) the annual occurrence of Hudsonian Godwits in New Zealand and eastern Australia (but their absence from mainland Asia) can best be explained by their accompanying Bar-tailed Godwits on a trans-Pacific flight; (5) birds appear energetically and mechanically capable of such a flight based on current knowledge of aerodynamics and measured fuel sources; and (6) known departures from Alaska coincide with favorable winds for a southward flight but are in opposition to a more south-westerly continental route. Aspects of several of these lines of evidence warrant additional discussion.

Factors constraining flight range

The simulations with program Flight suggest that even under still air conditions Bar-tailed Godwits leaving staging sites in Alaska with realistic body and fat mass values should be able to reach New Zealand in a non-stop flight of between 9 800 and 10 700 km. If the godwits are able to use tail winds routinely en route (see below), we can relax the assumption of a body drag coefficient of 0.05 (but see Elliott *et al*. 2004) and accept a value closer to the more often used 0.1 (Kvist *et al*. 2001, Pennycuick & Battley 2003). In addition to fat as fuel, protein availability and water (dehydration) can limit flight range (Klaassen 1995, Jenni & Jenni-Eiermann 1999). For the *L. l. taymyrensis* subspecies during a 4 300 km-long northward flight from western Africa to Europe, Landys *et al*. (2000) concluded that

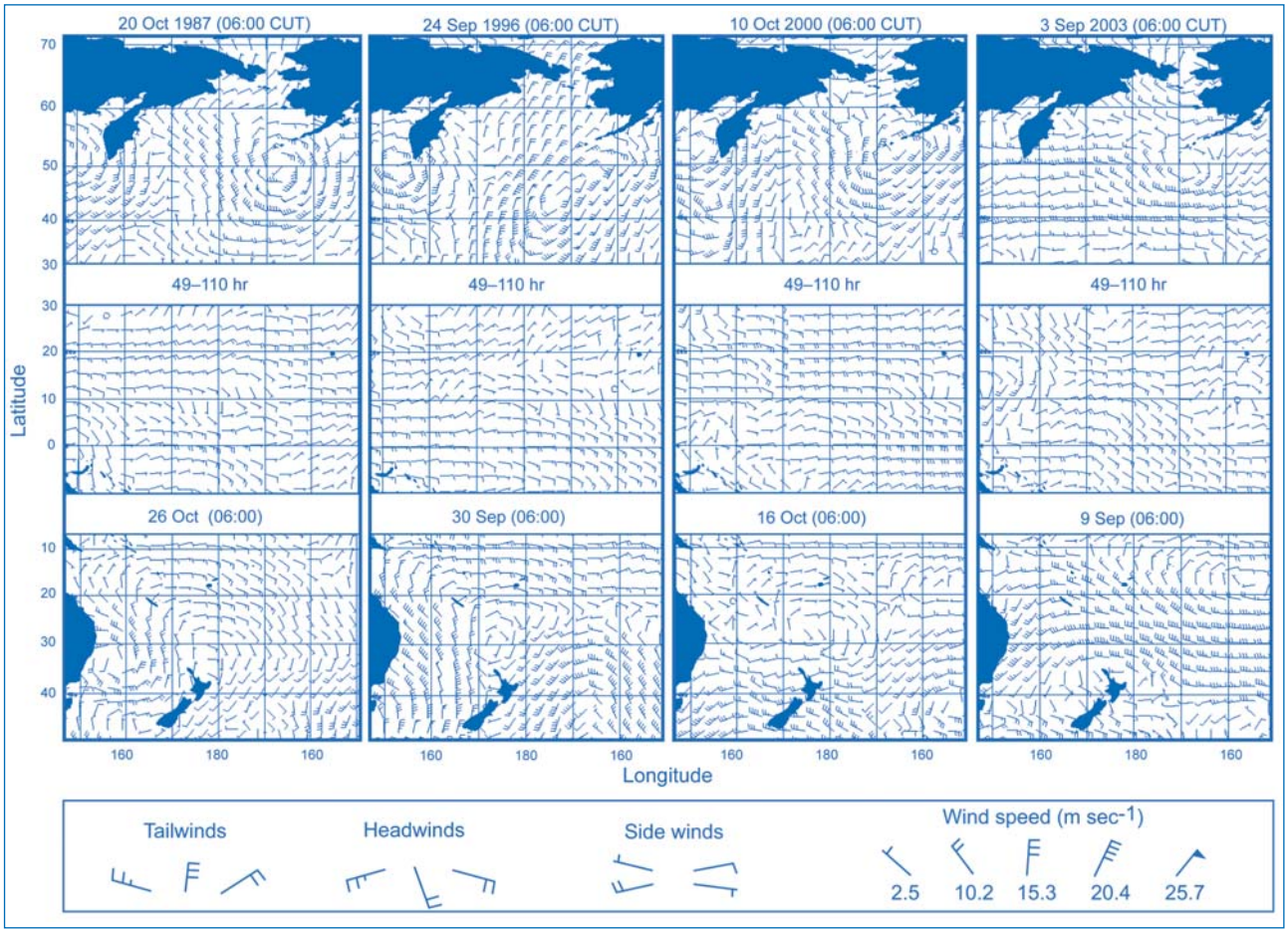

Fig. 5. En route winds (850 mb altitude) associated with the four recorded departures of Bar-tailed Godwits *Limosa lapponica* from Alaska. See Table 3 for location of departure sites. The upper panels represent winds at time of departure (± 3 hr, CUT = Coordinated Universal Time), middle panels show typical conditions between the 49th and 110th hr of the flight, and lower panels the conditions at the end (but are also representative of the preceding 24-36 hr). The long, unflagged portion of the axis of each wind bar points towards the direction the wind is blowing; the number and type of short flags perpendicular to the long axis of each wind bar indicate wind speed. The original wind vectors are depicted in knots and converted here to m sec^{-1}. The legend indicates the range of directions that would be tail winds, head winds, or side winds along the proposed trans-Pacific migratory corridor between Alaska and eastern Australia and New Zealand.

flights ranging in altitude from sea level to 3 000 m would avoid dehydration, and in fact found no evidence for dehydration in arriving godwits. Interestingly, Landys *et al*. (2000) also had to assume a body drag coefficient as low as 0.05 for the virtual godwits to complete their flight.

Our simulations have made clear that the necessary minimum protein use during non-stop flights does limit maximum flight range. Birds leaving Alaska with a lean mass lower than 275 g are predicted to have exhausted their fat when their lean mass is as low as 200 g and their pectoral muscles have become tiny (Table 4). The small-sized juvenile Bar-tailed Godwits with a lean mass of only 166 g and a fat store of 200 g that died during a collision probably just after take-off on a southward flight (Piersma & Gill 1998) are predicted (using the assumptions listed in Table 1) to be able to cover more than 11 000 km non-stop. Not surprisingly, they are also predicted to arrive with perhaps unrealistically low lean and pectoral muscle masses (for a body drag coefficient of 0.05, lean mass after 11 000 km of flight under still air conditions would be 170 g and pectoral muscle mass 25 g; with a coefficient of 0.1, the predicted final mass values are 130 g and 20 g, respectively). Given such values upon arrival in New Zealand, it seems unwarranted to expect these birds to have been capable of reaching the South Pole, an additional distance of 6 000 km, as predicted by Pennycuick & Battley (2003) who accommodated unrealistic lean mass values. Lowering the minimum energy obtained from protein to 2% does not resolve the problem. In view of the absence of hard data on body composition for adult godwits, and the problematic departure condition of the juveniles from 1987, detailed studies on body condition at departure in relation to performance during the ensuing flight and pin-pointing the exact arrival time in New Zealand are clearly needed.

A direct route or one with stopovers?

A direct flight by a congener

Hudsonian Godwits breed in subarctic and temperate North America and migrate to southern South America (Elphick & Klima 2002), yet are rare annual visitors to New Zealand (Higgins & Davies 1996, Elphick & Klima 2002) and occasionally elsewhere in Oceania (Watling 2001), with up to nine different individuals seen in a single year. What might explain the regular appearance of this species a hemisphere removed from its normal non-breeding range? It is highly unlikely that the Hudsonian Godwit, although also a long-distance migrant

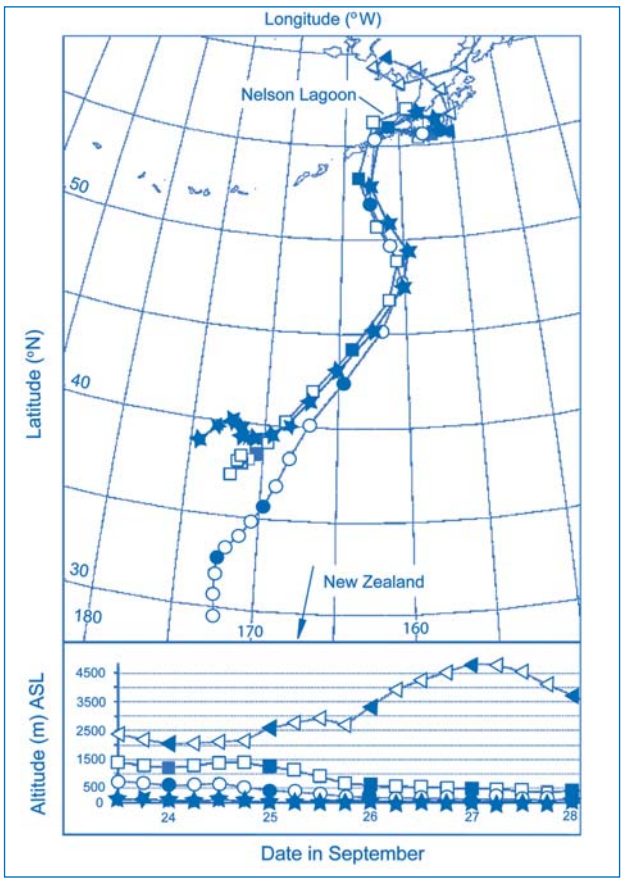

Fig. 6. Air flow over a five-day period for objects entering the air column at Nelson Lagoon, Alaska, at the time of the observed departure of Bar-tailed Godwits *Limosa lapponica* on 23 September 1996. The objects, entered into the air column at various altitudes, are then tracked at successive six-hour intervals; filled star = surface, unfilled circle = 750 m, unfilled square = 1 500 m, and unfilled triangle = 2 500 m elevation above sea level (ASL). Their respective filled symbols denote 24-hour periods. During the initial 60 hours of the model run between Nelson Lagoon and about 40° N latitude, winds at 750 m and 500 m altitude varied between 10 and 15 m sec^{-1}. The arrow to New Zealand approximates the direction but not necessarily the route taken.

(McCaffery & Harwood 2000), reaches southern Oceania by following a continental route via the east Asian mainland, a distance of over 16 000 km. Indeed, we could find only a single record of the species from Asia, and that from Chukotka, almost 150 years ago (in Kessel & Gibson 1978). It is also highly unlikely that birds reach New Zealand via a 9 000 km-long flight across the Southern Ocean after an initial flight of 8 000 to 11 000 km from eastern Canada to southern South America. The most logical explanation for their occurrence in New Zealand is that they accompany Bar-tailed Godwits on the godwits' southward flight across the Pacific (see also Kessel & Gibson 1978). Recent observations of small numbers of Hudsonian Godwits (all juveniles to date) support this idea.

Stopovers

As it is energetically more favorable to cover a certain migration distance in many small steps than in one long hop (Piersma 1987), the assembled evidence that some 150 000 Bar-tailed Godwits annually make an 11 000 km-long non-stop flight from Alaska to New Zealand/eastern Australia begs the question of why do they not make stopovers, either along the east Asian mainland, if such a route is followed, or during a trans-Pacific crossing. First, the evidence we have assembled fails to support use of a continental route, with or without use of stopover sites. Given the paucity of records of *baueri* along the east Asian mainland during southward migration, if they were migrating along the Asian coast, this would entail a non-stop flight of almost 16 000 km, i.e. 40% longer than a flight directly across the Pacific. Such a long flight is improbable, given the fuel loads of departing godwits and predicted arrival mass upon fuel depletion (contra Pennycuick & Battley 2003). In addition, during the recorded departures, birds would have initially encountered moderate to strong head winds and then a long fetch of strong southerly winds if they had followed a more south-westerly route along the Asian mainland. Such a flight would have forced birds either to fly into opposing winds or to detour around the systems, both of which would have added substantially to energetic costs.

We likewise found no evidence suggesting use of intermediate stopover sites if birds followed a direct route across the Pacific. Arguably, the Pacific Ocean is vast and it could harbor yet undiscovered stopover site(s), but the region has received considerable attention from ornithologists, and its indigenous peoples are intimately in tune with their natural resources. We find it beyond reason to expect the annual use by 150 000 godwits at stopover site(s) in Oceania to have gone undetected by either group of people. Indeed, the 80-year span of records that we searched accounted for a total of only about 4 000 godwits having been recorded throughout all of Oceania – this from a projected total of some 12 million godwits that could have stopped somewhere en route during this period. Although we cannot rule out that birds alight on open ocean waters during transit, it is likely that this would be for relatively short periods and then related to adverse conditions (Piersma *et al*. 2002) and not for rest.

Thus, a single flight over the Pacific is not only likely but in several ways advantageous as it may be safer (there are rarely aerial predators in central Oceania; cf. Ydenberg *et al*. 2002), healthier (as encounters with pathogens will be avoided; Piersma 1997), and faster and more direct (as the time required to settle at new stopover areas is avoided; Alerstam & Lindström 1990). It could also indicate the high quality of the western Alaskan staging sites relative to potential staging/stopover areas along the east Asian coastline or throughout Oceania (Gill & Handel 1990, Gudmundsson *et al*. 1991). Indeed, soft substrate intertidal habitat, the preferred feeding substrate for non-breeding godwits, is extremely limited throughout Oceania, occurring mostly on Fiji, the one site in Oceania that regularly hosts godwits (Watling 2001). See Gill *et al*. (2005) for a more detailed discussion of this topic.

The role of wind systems over the Pacific

The *baueri* subspecies of the Bar-tailed Godwit can be added to a growing list of birds that have evolved wind-sensitive migration strategies, especially southward migrations, within the subpolar marine low pressure belt that circles the Northern Hemisphere (Richardson 1979, Åkesson & Hedenström 2000, Green 2003, M. Green and T. Piersma unpubl. data). This phenomenon is especially evident in the North Pacific, where the Aleutian low pressure system shapes and dominates weather and wind patterns

throughout the year (Christoforou & Hameed 1997, Overland *et al*. 1997). In particular, two taxa of large-bodied, medium-distance migrant geese, the Brent Goose *Branta bernicla* and Cackling Canada Goose *B. canadensis minima*, annually initiate trans-oceanic flights from the Alaska Peninsula to the Pacific coast of North America in conjunction with the passage of moderate to strong low pressure systems (Dau 1992, Gill *et al*. 1997). Not surprisingly, even small-bodied birds, such as the Dunlin *Calidris alpina*, with similar non-breeding ranges often depart on the same weather systems as those used by geese (Warnock & Gill 1996, R. Gill unpubl. data). The emerging pattern is that godwits, geese, and Dunlin can use the same storms, only varying their departures in accordance with the position of the storm center and the birds' final destination.

Evolving a migration system in conjunction with winds at the departure site is one thing, but in the case of godwits which are crossing the entire Pacific, they must pass through at least five other latitudinal zones of defined winds and pressure. It is beyond the scope of this paper to present a thorough analysis of wind conditions along the entire projected flight path (cf. Piersma & Jukema 1990, Piersma & van de Sant 1992, Åkesson & Hedenström 2000). However, what emerges from the four cases we studied suggests that winds were generally favorable throughout the migration corridor during the calculated six-day transit time, and certainly in no instance was there strong opposing wind for any appreciable distance. The most obvious question relating to this is to what extent local departure cues are related to favorable "downstream" winds. Is weather across the Pacific structured (teleconnected) such that certain departure cues at northern latitudes translate to assure relatively favorable conditions along most of the route (McCaffery & Gill 2001)? The Aleutian low pressure center is a large-scale dominating feature of the North Pacific (Christoforou & Hameed 1997, Overland *et al*. 1997) that has obviously shaped the evolution of equally large-scale geographical migration patterns similar to systems described elsewhere in the Northern Hemisphere (citations in Green 2003). However, the godwits' migration strategy, involving flights that span hemispheres, is unlikely to have been selected for solely on the basis of factors occurring over just a portion of the range and independently of those elsewhere along the migration corridor.

This raises obvious questions about global climate change and its affects on wind regimes and thus on wind-selected avian migrants. The ecological effects of climate fluctuations are many, and are projected to be most profound in regions with large-scale patterns of climate variability such as the North Atlantic and North Pacific (Stenseth *et al*. 2002). Models of global climate change suggest an intensification of propagating weather systems moving across the North Pacific. Such would result in a shift of the Aleutian Low center eastward that would in turn increase the number and intensity of storms and bring stronger northerly winds over a longer fetch on the backside of individual low pressure centers. Godwits may, however, be able to adapt to this as the Aleutian Low and adjacent Hawaiian High have been found to shift position and intensity (seesaw pattern) on a decadal scale during most of the twentieth century (Christoforou & Mameed 1997, Overland 1999). The phenomenon, however, also needs to be assessed in the Southern Hemisphere as well in terms of the teleconnection patterns between the two hemispheres.

Development of suitable remote-sensing satellite technology would greatly enhance our understanding of the complexity of the godwits' migration system and flight behaviour of long-distance trans-oceanic migrants in general. With such technology, answers would be forthcoming to questions about (1) mechanisms of orientation, (2) how birds select winds (vertical and lateral) at all stages of the flight, (3) whether they adjust air speed for wind drift, (4) whether they adjust air speed during the course of the flight, and (5) the extent to which they can assess and react to changes in downstream flight conditions.

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Program Flight (Windows version 1.13, July 2003) can be downloaded at: http://detritus.inhs.uiuc.edu/wes/pennycuick.html.

Bar-tailed Godwit *Limosa lapponica* – one of the world's extreme long-distance migrants. Photo: Paul Marshall.